

## Symposium

### Effects of Exotic Species on Soil Nitrogen Cycling: Implications for Restoration<sup>1</sup>

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**Abstract:** Ecosystem ecologists and restoration practitioners have become increasingly interested in the effects that invading species might have on soil processes. Invading species, particularly ones that differ from native species in traits that are likely to influence soil processes, may influence nitrogen cycling to such an extent that the legacy of the invasion persists long after invaders have been removed. We suggest that exotic species that are capable of altering soil nitrogen (N) pools, whether by augmenting ecosystem N through fixation of atmospheric N or by increasing rates of N losses, have the greatest capacity to interfere with restoration efforts. In contrast, cases where more subtle differences in tissue quality or quantity alter soil N fluxes but not total N pools may not exhibit a legacy long after removal of the exotic species. Given the challenges that invading species' effects on soils present to restoration efforts, it is important to develop predictions as to which invaders are likely to influence N dynamics after their removal and to develop techniques to minimize the influence of exotics on restored ecosystems.

#### INTRODUCTION

During the past decade, numerous investigators have documented the effects of invading species on soil nutrient characteristics and, more recently, on soil microbial communities. Recent research has shown that individual plant species, many of which are nonnative (also referred to here as exotic), are capable of altering soil organic matter and nutrient stocks, nutrient cycling rates, soil moisture content, and the pH and cation distribution of soils in invaded ecosystems (D'Antonio and Corbin 2003; Ehrenfeld 2004; Levine et al. 2003). Advances in the characterization of microbial communities in recent years has also led to the recognition that there are complex feedbacks between vegetation composition, soil microbes, and nutrient cycling (Balser et al. 2002; Knops et al. 2002). Such issues are of particular concern in the context of the restoration of invaded habitats. Effects of exotic species can be very dramatic; however, it is not yet clear how persistent species effects on soil processes are and how they might affect the likelihood of successful restoration of invaded sites. Some changes may be persistent after a species has been removed and may af-

fect the direction or rate of succession of postremoval vegetation.

In this article, we review the recent evidence that invasive, nonnative species influence soil nitrogen (N) dynamics and suggest hypotheses as to the effects of invasive species on efforts to restore invaded habitats. Although we limit our review to soil N, the effects of invaders have also been considered for a variety of other aspects of soil, including pH and cation distribution (e.g., Blank and Young 2002; Kourtev et al. 1998), soil carbon content (e.g., Ehrenfeld 2004), and microbial community composition (e.g., Kourtev et al. 2002). We separately consider the effects of species on soil N pools and fluxes and the likelihood that such effects are likely to persist after removal. We propose that increases or decreases in rates of N fluxes such as N mineralization or nitrification may be relatively easily reversed once the target species are removed and are therefore likely to be relatively unimportant for restoration. Exceptions include cases where changes in N fluxes are associated with the development of multiple, stable vegetation states. In contrast, we hypothesize that other changes, such as increases or decreases in total soil N, may persist for many years after removal, leaving legacies that managers must consider in their restoration plans. Some restoration procedures may be more effective at counteracting soil legacies.

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## EFFECTS OF INVADERS ON SOIL N DYNAMICS

**N Pools.** The invasion of woody N-fixing species into habitats that previously lacked woody N fixers, such as *Myrica faya* in Hawaii (Vitousek and Walker 1989; Vitousek et al. 1987) and *Acacia* spp. in South Africa (Stock et al. 1995; Witkowski 1991), has been shown to result in substantial increases in soil N pools. Because of its association with N-fixing microbes, *Myrica* is able to fix 18.5 kg N ha/yr as compared with 0.17 kg N ha/yr fixed by other known biological sources (Vitousek and Walker 1989; Vitousek et al. 1987). As a result, litter from *Myrica* had significantly higher N content than litter from the dominant native tree, *Metrosideros polymorpha* (1.33 vs. 0.56%), and significantly lower lignin–N ratio in litter (25.3 vs. 37.5). Examination of the total N in the forest floor plus soil under forests with and without *Myrica* revealed that the invaded sites had  $631 \pm 305$  g more N than uninvaded sites. A second and similar example is the invasion of *Acacia* spp. into South African habitats previously lacking N fixers (Stock et al. 1995; Witkowski 1991). Stock et al. (1995) found that soil N content was 1.7 and 2.7 times higher in invaded strandfeld and fynbos habitats as compared with uninvaded sites.

The examples above, as well as those of other N-fixing species that have invaded relatively low-fertility habitats, offer support for the hypothesis that N-fixing species are capable of exerting a strong effect on ecosystem dynamics (D'Antonio and Corbin 2003). Such N-fixing invaders, with their ability to dramatically increase soil N pools and increase soil N availability (Hart et al. 1997; Maron and Jefferies 1999; Vitousek et al. 1997), pose a daunting challenge for efforts to restore invaded habitats. Enhancement of N availability has been shown to favor fast-growing invasive species in a variety of habitats (e.g., Huenneke et al. 1990; Maron and Connors 1996; Vinton and Burke 1995), so increased soil N pools after invasion of N fixing species may tip the competitive balance in favor of other nonnative species even after removal of the N fixers (Corbin et al. 2004). For example, Maron and colleagues (Maron and Connors 1996; Maron and Jefferies 1999) documented that invasion of *Lupinus arboreus* into California coastal prairies shifts grassland composition from native perennial to exotic annual species. In the case of *Myrica*, Adler et al. (1998) found that fast-growing exotic grasses benefited relative to native grasses after death of the N fixer.

It is less well understood how long the legacies of N-fixing invaders on soil N pools persist, although there are indications that soil N availability is likely to remain

elevated in some ecosystems for at least several years and perhaps much longer. Maron and Jefferies (2001) found that soil N levels were higher in soils that had formerly been invaded by *L. arboreus*, as much as 35 yr before, as compared with uninvaded soils, for at least 5 yr after lupine removal, despite active management that included mowing and removal of aboveground biomass. The method by which the N fixer is removed likely plays an important role in the likelihood that N pools will remain elevated. For example, Haubensak et al. (2004) found that removal of Scotch broom (*Cytisus scoparius*) and French broom (*Genista monspessulana*) shrubs in coastal California, using multiple controlled burns, reduced soil N to a greater extent than did mechanical removal or a single fire. Further research in this area is required, such as the ongoing studies in Hawaii, to evaluate methods for removing *Myrica* that will result in the lowest legacy on soil N (R. L. Loh, unpublished data).

Invaders could also decrease total soil N stocks by altering disturbance regimes or through their effects on N uptake and N transformation rates. For example, changes in disturbance regimes, such as fire frequency (D'Antonio and Vitousek 1992), are capable of increasing short-term N availability or decreasing soil N stocks (or both) (for review see Wan et al. 2001). N can also be lost through leaching, when uptake by either plants or soil microbial biomass does not equal rates of cycling (e.g., Hooper and Vitousek 1998; Jackson et al. 1998). Differences in phenology and summertime activity between exotic annual grasses and native perennial grasses contribute to elevated leaching losses of N in coastal California ecosystems dominated by the annuals (Maron and Jefferies 1999; J. D. Corbin and C. M. D'Antonio, unpublished data). We have documented lower soil percent N and slower net rates of N cycling in experimental plots dominated by annual grasses as compared with perennial grasses (J. D. Corbin and C. M. D'Antonio, unpublished data), indicating that N fluxes and N stocks are capable of interacting. However, even where species invasion is capable of altering rates of N cycling, the relative changes in N production and uptake may balance in such a way that there is no increase rates of N loss. Windham and Ehrenfeld (2003) found that the replacement of short grasses, such as *Spartina patens*, by *Phragmites australis* in coastal marshes in eastern North America stimulated N uptake and speeded up net N mineralization rates by nearly 300%. However, the changes in N cycling in vegetation and soil appeared to be largely compensatory, so that net N loss from the ecosystem was not significantly different in ecosystems dominated by *S. patens* and *P. australis*.

**Soil N Fluxes.** Plant species composition can influence soil N fluxes, including affecting rates of mineralization and nitrification, and ultimately N leaching losses that reflect the balance of N transformation and uptake processes. In some cases, the changes in soil N transformations seen in stands where invaders dominate may be associated with changes in soil N stocks—as in the cases of *Myrica* in Hawaii (Vitousek and Walker 1989) and *Acacia cyclops* in strandfeld ecosystems in South Africa (Stock et al. 1995). In these cases, the invaders typically have very different litter chemistry (lower lignin–N ratios, higher %N) than the residents. More subtle differences between litter quantity or quality between invaders and residents may also lead to changes in N fluxes, even if N stocks are unchanged. For example, Vinton and Burke (1995) compared nutrient cycling in the soil beneath introduced annual grasses with that under native perennial species in short-grass steppe in Colorado. The authors found that soils associated with the invaders had higher rates of N mineralization and higher microbial biomass C than soils associated with the natives. The annual grasses invaded these sites after the addition of fertilizer more than 20 yr before their study and have continued to dominate the sites. The litter qualities of the invaders were higher than that of the natives, and the persistence of the invaders suggested a positive feedback between tissue quality and N cycling that was triggered by the original nutrient addition. Asner and Beatty (1996) found that soils under native shrubland in Mōlokaʻi Island, HI, associated with the African pasture grass *Melinis minutiflora* were consistently associated with elevated  $\text{NH}_4$  availability, as measured using ion-exchange resins. This was the case even where there was no evidence that disturbance had promoted invasion of *Melinis*.

However, differences in litter quality or quantity between native and nonnative or resident and invader species (or both) do not consistently lead to changes in N cycling rates. For example, Mack et al. (2001) found no effect of invasion by introduced pasture grasses (primarily *Schizachyrium condensatum* but also *M. minutiflora*) as much as 30 yr earlier on annual net N mineralization in a young woodland on Hawaii island that contained many of the same native woody plant species as the Asner and Beatty (1996) study. Similarly, Svejcar and Sheley (2001) found no consistent differences in the rates of N cycling between disturbed desert sites invaded by *Bromus tectorum* for nearly 40 yr and nearby undisturbed sites dominated by native perennial species with very different litter chemistry.

We hypothesize that, although nonnative species that do not fix atmospheric N may also influence soil N fluxes through differences in litter quantity or quality or phenology, such effects are likely to develop more slowly and revert to background levels more quickly than effects that are driven by differences in soil N stocks. A notable exception may be cases where nonnative species alter soil microbial composition (Kourtev et al. 2002; C. V. Hawkes and M. K. Firestone, unpublished data) and thereby influence soil N fluxes. However, more study is needed to assess the long-term effects of this pathway because microbial composition can change rather rapidly with vegetation change (Balser et al. 2002; Belnap and Phillips 2001). Belnap (unpublished data) suggests that soil microbial changes may not affect long-term succession in a Utah grassland.

Although changes in soil N fluxes may revert more quickly than changes in soil N stocks, interactions between N cycling dynamics and species composition may still have dramatic effects. Wedin and Tilman (1990) suggested that positive feedbacks, whereby species influence N availability, which in turn influences species composition, could facilitate multiple, seemingly stable states under identical abiotic conditions. However, although frequently proposed, positive feedbacks between species effects on soil processes and vegetation composition have not been well described.

## IMPLICATIONS FOR RESTORATION

The capacity of invasive nonnative species to affect soil N dynamics is a daunting challenge for efforts to restore invaded habitats. We suggest that species that are capable of altering soil N pools, whether by augmenting ecosystem N through fixation of atmospheric N or by increasing rates of N losses, have the greatest capacity to interfere with restoration efforts. In contrast, exotic species that influence soil N fluxes through such mechanisms as differences in tissue quality or quantity, without altering soil N pools may not exhibit a legacy long after removal of the exotic species. However, these hypotheses remain largely untested. Indeed, our knowledge of the effects of exotic species on soil processes is limited in its ability to guide restoration efforts. Now that ecologists recognize that exotic species have the potential to exert significant effects on soil dynamics, the next step is to develop predictions as to which invaders are likely to influence N dynamics after their removal and to develop techniques to minimize the influence of exotics on restored ecosystems.

## LITERATURE CITED

- Adler, P., C. M. D'Antonio, and J. T. Tunison. 1998. Understory succession following a dieback of *Myrica faya* in Hawaii Volcanoes National Park. *Pac. Sci.* 52:69–78.
- Asner, G. P. and S. W. Beatty. 1996. Effects of an African grass invasion on Hawaiian shrubland nitrogen biogeochemistry. *Plant Soil* 186:205–211.
- Balser, T. C., A. P. Kinzig, and M. K. Firestone. 2002. Linking soil microbial communities and ecosystem functioning. In A. P. Kinzig, S. W. Pacala, and D. Tilman, eds. *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton, NJ: Princeton University Press. Pp. 265–293.
- Belnap, J. and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecol. Appl.* 11:1261–1275.
- Blank, R. R. and J. A. Young. 2002. Influence of the exotic crucifer, *Lepidium latifolium*, on soil properties and elemental cycling. *Soil Sci.* 167:821–829.
- Corbin, J. D., C. M. D'Antonio, and S. J. Bainbridge. 2004. Tipping the balance in the restoration of native plants: experimental approaches to changing the exotic:native ratio in California grassland. In M. Gordon and S. Bartol, eds. *Experimental Approaches to Conservation Biology*. Berkeley, CA: University of California Press. Pp. 154–179.
- D'Antonio, C. M. and J. D. Corbin. 2003. Effects of plant invaders on nutrient cycling: using models to explore the link between invasion and development of species effects. In C. D. Canham, J. J. Cole, and W. K. Lauenroth, eds. *Models in Ecosystem Science*. Princeton, NJ: Princeton University Press. Pp. 363–384.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23:67–87.
- Ehrenfeld, J. G. 2004. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*. 6:503–523.
- Hart, S. C., D. Binkley, and D. A. Perry. 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biol. Biochem.* 29:1111–1123.
- Haubensak, K. A., C. M. D'Antonio, and J. Alexander. 2004. Effects of nitrogen fixing shrubs in Washington and coastal California. *Weed Technology* 18:1475–1479.
- Hooper, D. U. and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68:121–149.
- Huenneke, L. R., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology* 71:478–491.
- Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1998. Plant and soil nitrogen dynamics in California annual grassland. *Plant Soil* 110:9–17.
- Knops, J.M.H., K. L. Bradley, and D. A. Wedin. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecol. Lett.* 5:454–466.
- Kourtev, P. S., J. G. Ehrenfeld, and M. Haggblom. 2002. Exotic plant species alter the microbial community structure and function of the soil. *Ecology* 83:3152–3166.
- Kourtev, P. S., J. G. Ehrenfeld, and W. Z. Huang. 1998. Effects of exotic species on soil properties in hardwood forests of New Jersey. *Water Air Soil Pollut.* 105:493–501.
- Levine, J. M., M. Villa, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of invasive species. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 270:775–781.
- Mack, M. C., C. M. D'Antonio, and R. E. Ley. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C<sub>4</sub> grasses in Hawaii. *Ecol. Appl.* 11:1323–1335.
- Maron, J. L. and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312.
- Maron, J. L. and R. L. Jefferies. 1999. Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology* 80:443–454.
- Maron, J. L. and R. L. Jefferies. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. *Ecol. Appl.* 11:1088–1100.
- Stock, W. D., K. T. Wienand, and A. C. Baker. 1995. Impacts of invading N<sub>2</sub> fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and <sup>15</sup>N natural abundance values. *Oecologia* 101:375–382.
- Svejcar, T. and R. Sheley. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. *J. Arid Environ.* 47:33–46.
- Vinton, M. A. and I. C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* 76:1116–1133.
- Vitousek, P. M. and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. *Ecol. Monogr.* 59:247–265.
- Vitousek, P. M., L. R. Walker, L. Whiteaker, D. Mueller-Dombois, and P. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–804.
- Wan, S., D. Hui, and Y. Luo. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol. Appl.* 11:1349–1365.
- Wedin, D. A. and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433–441.
- Windham, L. and J. G. Ehrenfeld. 2003. Net impact of a species invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecol. Appl.* 13:883–897.
- Witkowski, E.T.F. 1991. Effects of alien *Acacias* on nutrient cycling in coastal lowlands of the Cape Fynbos. *J. Appl. Ecol.* 28:1–15.